1 The structure of plant–pollinator networks is affected by crop

2 type in a highly intensive agricultural landscape

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13 Abstract

14 In agricultural landscapes, bipartite networks formed by pollinators and the flowers they

15 forage on, are characterised by the presence of species managed by humans, whether

16 honeybees (*Apis mellifera*) or crop plants. These managed species can affect the structural

17 properties of these networks because of spatial and temporal variation in the availability of

18 resources, and competition for these resources; for example, crop plants such as oilseed rape

19 and sunflower produce a large number of flowers during a short blooming period. Here, we

20 examined the structure of plant–pollinator networks in an intensive agricultural landscape, the

21 LTSER Zone Atelier Plaine & Val de Sèvre (West of France). We compiled a six-year

22 monitoring dataset of plant–pollinator interactions, sampling by sweep-nets along transects in

23 the main six crop types (811 fields in total). To describe networks, we computed six metrics:

24 connectance, nodes number, modularity, specialisation and two nestedness measures. Strong

25 differences between crops were observed in nestedness and specialisation: in oilseed rape,

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26   networks were much more nested and much less specialised than in sunflower. In addition,

27   the link 'honeybee–crop flower' differed between the two mass-flowering crops. Honeybees

28   and sunflowers appeared as specialist species in sunflower crops, interacting strongly and

29   almost exclusively with each other, whereas they are usually considered highly generalist

30   species. Indeed, sunflower pollination may be almost entirely driven by honeybees,

31   conversely to oilseed rape crops, where the presence of wild bees and other insects tended to

32   produce a more diversified network.

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Key words

35   Bipartite networks, Mass-flowering crops, Weeds, Honeybees, Spatio-temporal heterogeneity

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Highlights

38   • Honeybees and crop flowers drive the network structure in agricultural environment

39   • Main mass-flowering crops got very distinct network properties

40   • Specialisation of managed species is highly variable among mass-flowering crops

1. Introduction

Insect biodiversity is declining worldwide, and numerous local insect extinctions have already

been documented (Habel et al., 2019). This decline has high consequences for the ecosystem

services that rely upon insects, not least pollination (Frankie et al., 2009). In temperate

regions, 88% of plants depend on zoogamous pollination for their reproduction (Ollerton et

al., 2011) and 70% of crops depend to some extent on insect pollination (Klein et al., 2007),

which improves yields of insect-pollinated crops and ensure agricultural production, as in

oilseed rape (OSR; *Brassica sp.*) and sunflower (SF; *Helianthus sp.*) (Perrot et al., 2019,

2018). In arable farming systems, insect pollinators forage partly – and sometimes mainly –

on mass-flowering crops, but availability of these crops does not cover the entire season of the

pollinators' activity (Odoux et al., 2014). Between OSR and SF blooms (the so-called 'dearth

period'), the resources provided by weeds are essential for maintaining pollinators, including

the honeybee *Apis mellifera* (Carvalheiro et al., 2011; Requier et al., 2015). Weeds and other

wild plants are therefore critical for pollinators (Bretagnolle and Gaba, 2015), and contribute

to their diversity and abundance at both field and landscape scales (Carvalheiro et al., 2011).

Among insect pollinators, bees and hoverflies contain generalist species that can interact with

many wild flowers (Dunn et al., 2020) or crop plants, and both improve pollination service

(Garibaldi et al., 2011). Hoverflies are more resilient to agricultural modifications than bees in

agricultural landscapes (Jauker et al., 2009); conversely, butterflies which also pollinate many

wild plants, have been dramatically affected by agricultural intensification (Johst et al., 2006).

Overall, weeds and pollinators are closely intertwined in agricultural farmland, and form

ecological interaction networks, defined by a set of nodes (species) interconnected by one or

more links (interactions). There is evidence that such networks have changed in structure over

the last century, due to pollinator and plant community changes, with many interactions

involving specialist species being lost (Mathiasson and Rehan, 2020), mostly as a result of

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66 land use intensification (Ferreira et al., 2013). Indeed, the persistence of pollinators – together

67 with the services they provide – depends on stability, hence the structure of plant–pollinator

68 ecological networks.

69 However, plant–pollinator ecological networks in agricultural landscapes present unique

70 properties: first, they harbour managed and over-abundant species; second, they are highly

71 dynamic in space and time due to crop rotations. Such characteristics are expected to impact

72 the nature and structure of plant–pollinator networks. First, farmland ecological networks are

73 structured around managed honeybees in addition to wild pollinators, and managed crops in

74 addition to weeds (Geslin et al., 2017). The effect of mass-flowering crops on one hand, and

75 the presence of the honeybee on the other hand, can be related to 'invasive species' in arable

76 systems (Geslin et al., 2017; Stanley and Stout, 2014), i.e. super-generalist species that

77 interact with multiple groups of species (Giannini et al., 2015), leading to asymmetry and

78 nestedness of the network (Ferreira et al., 2013). Perhaps counterintuitively, this asymmetry

79 and nestedness contributes to the stability and the resistance of networks to land use change

80 (Memmott et al., 2004). Links that emerge from these super-abundant species may, however,

81 come at the expense of others, leading to species role shifts (Albrecht et al., 2014), or even

82 loss of species in both plants or pollinators, which should affect the structure and functioning

83 of networks (Valido et al., 2019). For instance, OSR flowers number c. 500,000/ha (Hoyle

84 and Cresswell, 2007), are brightly coloured and attractive, and produce both pollen and

85 nectar. OSR can thus create a distortion in mutualistic networks and has already been shown

86 to be related to the decline of specialist long-tongued bumblebees in favour of short-tongued

87 species better adapted to its flower traits (Diekötter et al., 2010). Honeybees in return may

88 decrease wild bee richness, leading to networks with fewer links (Lázaro et al., 2021).

89 However, a decrease or even a removal of supergeneralist (key) species may destabilise the

90 network (Kovács-Hostyánszki et al., 2019). Secondly, agricultural landscapes display very

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91   high spatio-temporal unpredictability (due to crop rotations), and seasonal heterogeneity

92   (Rollin et al., 2016): honeybees are present from April to September (Odoux et al., 2014),

93   while OSR and SF, the main super-generalist plants, have very short flowering peaks

94   (Bretagnolle and Gaba, 2015), and wild bees show generally have a short presence within the

95   season. Crop rotation and spatial heterogeneity is therefore expected to affect the temporal

96   and spatial dynamics of plant–pollinator networks (Chakraborty et al., 2021).

97   There is currently a lack of descriptive information on plant–pollinator networks in farmland

98   habitats, especially at large spatial scale or over longer time-scales (Olesen et al., 2011).

99   Indeed, most studies investigated the crop compartment in relation to the semi-natural

100   elements or its plants (e.g. Magrach et al., 2018; Stanley and Stout, 2014), while few studies

101   aimed at investigating differences among crops (but see Kovács-Hostyánszki et al., 2019) and

102   even fewer the effect of crop diversity. This is unfortunate, since crop effect was found to be

103   the most statistically important effect in a vast study of predation–prey networks in

104   agricultural habitats (Ma et al., 2019). Indeed, descriptive information is critical to

105   understanding community stability and robustness, which are linked to the number of species

106   and the number of links between them (Carpentier et al., 2021), and therefore network

107   resilience, which relies on redundancy in the number of pollinator species per plant species

108   (Memmott et al., 2004) and network nested structure (Bascompte et al., 2003). Network

109   stability is improved by pollinator diversity (Bendel et al., 2019), nestedness and low

110   modularity, though possibly at the expense of persistence (Thébault and Fontaine, 2010).

111   Along environmental gradients from less- to more- impacted by human footprint, e.g. from

112   natural sites to monoculture farming, an increase in connectance and nestedness but a

113   decrease in the number of nodes as well as modularity were shown (Morrison et al., 2020).

114   Increased connectance is expected to decrease secondary extinctions (Blüthgen et al., 2007)

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115   and improves robustness at the community level as well as stability (Thébault and Fontaine,

116   2010).

117   In this study, we used a descriptive approach to qualify plant–pollinator networks in a highly

118   intensive farming system, at a large spatial scale (study site of 450km²) with data collected on

119   six different crop types (811 fields in total). Because our sampling effort was high, we first

120   paid attention to two generally overlooked patterns, the effect of sample size and the degree

121   distribution. Sampling effort has been shown to affect many network metrics, through

122   sampling intensity and sampling bias, but also underlying species abundances (Blüthgen et

123   al., 2007). Degree distribution is highly skewed, resulting in part from many 'forbidden links'

124   (Jordano, 2016). The frequency distribution of links is claimed to be best described by power-

125   law distributions (Blüthgen, 2010), which have been shown to fit most natural networks. We

126   also describe the overall visual structure of networks by seasons and crop types. Then, we

127   investigated major features of the network, from simple network descriptors (number of

128   nodes, connectance) to more complex ones (nestedness, modularity, specialisation),

129   quantifying their level of variation among crop types and seasons, while accounting for

130   sample size. We expected plant–pollinator network structure to vary seasonally because of the

131   presence of mass-flowering crops, and the spillover or dilution effects that result from such

132   presence. Indeed, we expected strong variations in network structure among crop types, in

133   particular between mass-flowering and other crops, but also between arable crops and

134   grasslands. We further predicted a clear dominance of the managed honeybee, especially

135   during the flower blooms of OSR and SF, which dominate landscapes when flowering. In

136   particular, we predicted that networks would be more specialised during OSR and SF blooms

137   than in other periods and other crops. We also predicted that networks would be more nested

138   during the blooming periods of mass-flowering crops than in the dearth periods, and thus in

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139 these crops – as a result of super-generalist and abundant species presence – more able to

140 include the same partners as the specialists in their spectrum of interactions.

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2. Materials and methods

2.1. Study site

144 Our study site is the Long Term Socio-Ecological Research (LTSER) site 'Zone Atelier

145 Plaine & Val de Sèvre', located in the Nouvelle-Aquitaine region of southwest France, south

146 of the city of Niort (Bretagnolle et al., 2018). It covers 450 km², harbouring c. 13,000 fields.

147 We focused on six years of survey, 2015–2020, which is one of the largest time intervals of

148 plant–pollinator network studies (but see Chacoff et al., 2018; Petanidou et al., 2008; Ponisio

149 et al., 2017). Each year, 100 to 220 different fields were surveyed (some fields were studied

150 for more than one year) with a standardised protocol. Fields were selected in a stratified

151 random process (see Bretagnolle et al. (2018) for details). From 2015–2020, the number of

152 fields sampled per respective year were 174, 217, 195, 160, 117 and 115 (see ESM1a and 1b

153 in Appendix A). Crop surveyed included 7% corn (*Zea mays*) and sorghum (*Sorghum*

154 *bicolor*), 8% alfalfa (*Medicago sativa*), 12% meadows (temporary or permanent), 18% oilseed

155 rape (*Brassica napus*), 22% sunflower (*Helianthus annuus*), and 33% cereal crops. Cereals

156 included barley (*Hordeum vulgare*), durum wheat (*Triticum turgidum*), einkorn (*Triticum*

157 *monococcum*), oat (*Avena sativa*), rye (*Secale cereale*), triticale (*×Triticosecale*) and winter

158 wheat (*Triticum aestivum*). Sampling was performed from April to August, i.e. all crops were

159 surveyed at least once during their respective flowering periods: OSR from April–May;

160 sunflower from July–August; alfalfa, meadows and cereals from May–June to the end of

161 August; and corn and sorghum from July–August.

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2.2. Sampling of plant–pollinator interactions

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164   Insects surveyed included bees (both honeybees and wild bees), butterflies and hoverflies

165   (Syrphidae), i.e. the three main pollinator groups in the LTSER. This study site hosts a large

166   number of pollinator species (Rollin et al., 2016). Each year, two (2015) or three (2016–2020)

167   50 m long transects were performed per field: one in the field centre, one in the field margin

168   (section between the field edge and the first seeding line) and the last in between, at c. 25 m

169   from the margin (except in 2015). Field margins generally harbour a more diverse fauna

170   compared to field cores. Transects were parallel to tram lines. For each transect, the surveyed

171   area was a theoretical volume, 2.5 m each side, 2.5 m in front of the observer and c. 1 m

172   above the observer's head. Surveys were conducted under calm weather conditions, i.e. sunny

173   days with air temperatures in full sun mostly above 15°C (95% T >16°C; 12° to 45°C, in

174   sunlight), and between 7:30 a.m. and 6:30 p.m. In 27.9% of the fields (226 of 811), two

175   sampling sessions were conducted (early- and late-season). Each plant–pollinator interaction

176   (i.e. an insect landing on a flower) was tallied, with both plant and pollinator being identified

177   (pollinators being caught with a sweep-net for later identification by a professional

178   entomologist if necessary). Transects were walked along very slowly (c. 12 s/m), for a total

179   duration of 10 min each. The observer stopped the timer each time an insect had to be

180   identified or captured. Butterflies were always identified by sight; however, given the time

181   spent in flight in butterflies, all individuals crossing the sampled theoretical volume were

182   tallied, even if not on a flower. Almost all pollinators and plants (94% and 96% respectively)

183   were identified to species level.

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185   **2.3. Statistical analyses**

186   *2.3.1. Sampling completeness and frequency distribution of degrees*

187   We estimated sampling completeness of plants and pollinators using the Chao estimator of

188   asymptotic species richness (Chacoff et al., 2012), which is based on rare species (those that

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189   occur only once or twice). We calculated the Chao 2 estimator using the *vegan* R package

190   (v2.5.7; Oksanen et al., 2020) and evaluated the percentage of completion (ratio between the

191   observed value and estimated value) of our sampling of plants and pollinators.

192   We analysed the frequency distribution of degrees in total as well as in subnetworks (per crop

193   and per period), testing for best-fit with *a priori* distributions, i.e. Exponential, Poisson,

194   Weibull, Lognormal, Negative binomial, Power law and Fisher's logseries. We used the

195   *fitdistrplus* package (Delignette-Muller and Dutang, 2015), except for the Fisher's logseries

196   (which is not implemented in this package), which we computed. Power law was tested with

197   the *poweRlaw* package (Gillespie, 2015). Best fit was checked using the Akaike Information

198   Criterion (AIC; Burnham et al., 2011). We fixed a threshold of 2 units' difference in AIC to

199   select the best model among the candidate models.

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201   *2.3.2.   Number of nodes and number of interactions: crop and temporal effects*

202   From floral visitation events, we constructed bipartite networks with plant and bee nodes,

203   using a visitation event as a plant–pollinator interaction. To analyse how the network structure

204   varied among crops and seasons, we built interaction subnetworks. Six crop categories were

205   retained: OSR, cereals, alfalfa, meadows, SF and corn–sorghum. We also split the data into

206   three equal-length seasons, each 45 days long: April 1st–May 20th (OSR flowering peak,

207   characterised by high resource availability for insects), May 21st–July 9th, characterised by a

208   general lack of flowering crop resources available (i.e. the dearth period) – when honeybee

209   colony sizes are, perhaps surprisingly, at their highest (Odoux et al., 2014) – and finally, July

210   10th–August 22nd, corresponding to the SF flowering peak. We also divided our dataset into

211   six main taxonomic groups: honeybees, bumblebees, other social bees (including some

212   *Halictidae*, e.g. *Halictus rubicundus*, *Lasioglossum pauxillum*), solitary bees, hoverflies and

213   butterflies. To describe seasonal patterns in the number of interactions, we standardised our

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214 data, since the number of transects per field and the number of fields sampled per crop and

215 per year varied. We thus converted the number of interactions per transect per field into a

216 number per hectare (ha), since each transect surveyed an area of 250 m². Next, we grouped

217 samples per fortnight by averaging values (with standard-error, se) of interactions per ha per

218 fortnight for each crop. Obtained values were compared with ANOVA and post-hoc Tukey

219 tests. Data were log-transformed.

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221   *2.3.3. Network structure descriptors*

222 A large number of indices is available to describe network structure (see ESM2, which

223 presents their respective properties in Appendix A). We selected the following ones: number

224 of nodes (i.e. the number of species in interaction), connectance (the ratio between the number

225 of links observed and the total number of possible links), modularity – which gives insights

226 into the presence of subnetworks among the network (called modules, i.e. weakly interlinked

227 subsets of species that are constituted of strongly interacting species) and which was

228 calculated using the greedy Louvain algorithm method (Blondel et al., 2008) – and

229 nestedness, described by NODF (Nestedness metrics based on Overlap and Decreasing Fill;

230 Almeida-Neto et al., 2008). The latter is a property describing to what extent the partners of

231 specialists are a subset of the partners of generalists. We also used WNODF (Weighted

232 Nestedness metrics based on Overlap and Decreasing Fill; Almeida-Neto & Ulrich, 2011), the

233 quantitative alternative to NODF that accounts for the number of similar interactions. Finally,

234 we focused on the specialisation H_2' (standardised two-dimensional Shannon entropy) – the

235 degree of specialisation between the two levels of the entire network (Blüthgen et al., 2006) –

236 and the d' species-level specialisation measure (standardised Kullback–Leibler distance,

237 Blüthgen et al., 2006), corrected by de Manincor et al. (2020), representing the degree of

238 interaction specialisation at the species level. Network descriptors were obtained using the R

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239 packages *bipartite* (Dormann et al., 2009), *igraph* (Csardi and Nepusz, 2006), *NetIndices*

240 (Kones et al., 2009) and *vegan* (Oksanen et al., 2020).

241 Some of these metrics (i.e. connectance, nestedness) are sensitive to sample or network size

242 (Dormann et al., 2009). We thus checked how indices varied with increasing numbers of

243 samples (according to periods and crops) by calculating all metrics (excluding d') with

244 increasing numbers of sampled fields. Five to 195 fields (every 10 field steps) were randomly

245 sampled (with replacement) from the overall sample. At each step (i.e. field number), 100

246 groups of fields were constituted, the six network metrics were computed and the mean and

247 the 95% confidence interval (CI) were calculated. The maximum bootstrap threshold to

248 compare the three seasons was 175 field groups, when OSR period samples stopped, but we

249 also went up to 195 fields to compare only dearth period and sunflower period. When

250 comparing the six different crop types, we had to stop at a threshold of 35 fields per group

251 (100 groups) in the bootstrap because we had very few fields of corn–sorghum and alfalfa. To

252 increase the sampling effort, we had to lose crops, and were left with only four crops with 100

253 groups of 85 fields. However, when focusing on the two mass-flowering crops, OSR and SF,

254 we were able to analyse 100 groups of 165 fields. Therefore, the number of fields

255 bootstrapped varied according to the crops to be compared.

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257   *2.3.4. Field selection*

258 To calculate Chao 2 estimates and the number of interactions per hectare, we included the

259 fields in which no insects had been observed (138 fields, 17.0%). However, to represent

260 interaction networks and calculate metrics on aggregated fields, we only retained the fields on

261 which at least one interaction was observed in the dataset.

262 All analyses were run with *R software v.4.1.0* (R Core Team, 2021).

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3. Results

3.1. Sampling completeness and frequency distribution of degrees

A total of 37,133 plant–pollinator interactions were tallied over 811 fields (127 of which were studied in at least two years between 2015 and 2020), occurring between 200 species of pollinators foraging on 165 species of plants (including individuals that were only identified to genus level). We found 96 species of solitary bees, 35 species of social bees (including the honeybee *A. mellifera* and 14 species of bumblebees), 38 species of butterflies and 31 species of hoverflies. A total of 758 interactions were obtained between one plant or one pollinator occurring only once. No interaction was found between one plant and one pollinator occurring both only once. In regard to pollinators, over the full network, 80 species (40.0%) interacted with only one plant (crop or weed), 29 species (14.5%) interacted with two, while 91 species (45.5%) were more generalist (>2 plants, up to 92 plants). Similar values were obtained for plants, with 38 weed species interacting with only one insect species (23%), and 16 with two insect species (9.7%). There were 138 fields without any observed interaction (17.0%). We caught 64.5% of pollinators, and recorded 78.6% of the plant community, based on Chao 2 estimators.

Overall, the frequency distribution of degrees (i.e. interacting plants/pollinators) fitted better to the Fisher's log-series (see ESM3 in Appendix A) than to Lognormal ($\Delta_{AIC} = 73$) or Power laws ($\Delta_{AIC} = 77$). When splitting by crop or per season, similar results were found. Differences in the goodness-of-fit of Fisher's log-series and Lognormal were, however, much lower in alfalfa ($\Delta_{AIC} = 12$) and in corn and sorghum crops ($\Delta_{AIC} = 3$) than in other crops.

3.2. Number of nodes and number of interactions: crop and temporal effects

The total number of nodes varied highly among crops (165, 114, 186, 178, 161 and 75 in meadows, alfalfa, cereals, SF, OSR and corn–sorghum, respectively). Accumulation curves

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289   per crop indicated that these differences among crops (Fig. 1) could be detected even from

290   low sample sizes (c. n = 50). Thus, independently of the number of sampled fields, meadows

291   showed the highest values of node numbers, followed by alfalfa, cereals, OSR and SF (Fig.

292   1). Year did not affect the pattern of the accumulation curves (see ESM4 in Appendix A),

293   although 2017 was a species-rich year regardless of the sampling effort.

294   The number of plant–pollinator interactions, here standardised per hectare of sampling effort

295   (which can be considered as an instantaneous visitation rate per hectare), was on average

296   338.43 ± 23.19 interactions/ha (mean±se). This value, however, showed strong seasonal

297   variations, with most interactions occurring in early July when considering all crops, or mid-

298   June when excluding SF (Fig. 2). There were also strong variations among crops, with

299   interactions in SF being overwhelmingly dominant and driving seasonal variation. In early

300   July, we found significant differences in the average number of interactions among crops

301   ($F_{5,62} = 20.16$, p-value < 0.0001), with significantly higher values for SF than in alfalfa (T_{HSD}

302   p-adj < 0.001), meadows (T_{HSD} p-adj < 0.001), cereals (T_{HSD} p-adj < 0.001) and OSR (T_{HSD} p-

303   adj = 0.0015).

304   Network structure differed strongly among crops in relation to variation of the total number of

305   nodes, either in the repartition of interactions between the main groups of plants or between

306   the main groups of pollinators (Fig. 3). In flowering crops, the crop flower was generally the

307   most visited flower in the crop considered. For instance, 95.27% of pollinators visited SF

308   plant in SF fields, and 86.07% OSR plants in OSR fields. However, this was true only for

309   mass-flowering crops: alfalfa represented approximately a third of all visited flowers in alfalfa

310   fields (36.12%) and corn was poorly visited in corn–sorghum fields (7.55%). In those crops,

311   pollinators preferentially foraged on wild flowers (89.62%). Moreover, honeybees'

312   dominance was not of the same magnitude in all crops: they were overrepresented in SF

313   (91.95%) and OSR (76.60%), while hoverflies rather than honeybees were the most-

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314   interacting group in other crops (32.55% in corn and sorghum crops, 56.42% in cereal crops,

315   36.02% in alfalfa crops and 53.38% in meadows). Interestingly, when found in other crops,

316   OSR and SF flowers showed the same interaction pattern, i.e. interacting mainly with

317   honeybees. Moreover, hoverflies foraged more on wild flowers than did any other insect

318   group, potentially explaining their high presence in weed-rich crops such as meadows or

319   alfalfa. For instance, whereas the total percentage of weed visits by all pollinator groups was

320   63.78% in alfalfa crops, it reached 77.94% when considering only hoverfly visits.

321   The overall pattern of the network is depicted on Fig. 4, which represents standardised

322   interactions between pollinators and plants according to their degree (i.e. number of

323   interaction partners). Species with the highest degrees were not necessarily the most frequent,

324   although species' frequency of occurrence and degree were strongly related (i.e. decreasing

325   pattern of species degrees were concomitant with decreasing species frequencies) (Fig. 4). In

326   terms of the number of interactions, honeybees and bumblebees were most prevalent (83.72%

327   of the total interactions number, n = 31,089), followed by hoverflies (8.21%, n = 3,050),

328   solitary bees (2.69%, n = 998) and butterflies (1.36%, n = 506). Honeybees were by far the

329   dominant insect species (80.80% of all interactions, n = 30,007), the next two being

330   *Sphaerophoria scripta* (3.80%, n = 1,412) and *Episyrphus balteatus* (2.19%, n = 812), two

331   hoverflies. However, although *S. scripta* was found 20 fewer times than honeybees in total, its

332   number of plant partners (92) was higher than that of honeybees (75). Butterflies were far less

333   often observed, with only 81 interactions for the most common butterfly, *Pieris rapae*.

334   Concerning plants, SF represented 72.36% (n = 26,871) of the whole sample, seven times

335   more than OSR (10.69%, n = 3,971), and 60 times more than the most-interacting weed,

336   *Torilis arvensis* (1.20%, n = 446). Therefore, the complete network was dominated by

337   honeybees and mass-flowering crops: honeybees interacting with OSR or SF represented

338   77.44% of all interactions.

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3.3. Network structure

3.3.1. Seasonal effect on network structure

The average number of nodes during the dearth period (mid-May to early July) was similar to

the average number of nodes for all periods, regardless of the sampling effort (Fig. 5a),

reaching 214 ($CI_{95\%}$: 195–230) species when considering a sampling effort of 175 fields. The

average number of species was nearly equal during SF and OSR flowering blooms (154 (142–

165) and 148 (146–151), respectively, in 175 fields); that is to say, 1.4-times lower than

during the dearth period, but with a weaker variability among fields during OSR flowering.

Mean connectance did not vary a lot with period, being 3% (2.6–3.4) during bloom periods

and 2.5% (2.2–2.8) during the dearth period in 175 fields. Mean modularity was slightly

higher for the OSR blooming network (0.42 (0.41–0.43)) than for other periods (0.39 (0.36–

0.41) in SF blooming and 0.37 (0.35–0.38) in dearth period)). Specialisation of the network

remained constant during dearth and SF periods when considering network sizes above 100

fields (see ESM2 for details in Appendix A), but decreased much more quickly in the OSR

blooming period, with no overlapping 95% in CIs. This highlights that OSR blooming period

was represented by more generalist species than the other periods. Specialisation was higher

during the SF bloom and dearth periods, with average values between 0.49 (0.43–0.55) and

0.50 (0.46–0.52), respectively, compared to the OSR flowering bloom (0.30 (0.29–0.33)). The

OSR blooming period was characterised by a higher nestedness (37.2 (35.6-38.6) in 175

fields) than the SF blooming period (24.0 (21.3–26.9)) and dearth period (27.0 (24.4–29.9)).

Similar patterns were observed when using weighted NODF: 14.8 (12.7–16.8) during the

dearth period, 13.3 (11.8–15.0) during the SF blooming period, and 21.9 (20.6–23.1) during

the OSR blooming period. Thus, it seems that the flowering period of the OSR was the most

prone to host specialist species that had partners similar to generalist species.

15

364

3.3.2. Crop effect on network structure

366 All crops' subnetworks were similarly poorly connected (c. 3% at a threshold of 85 fields)

367 (Fig. 5b). Although OSR blooming period was the most modular period (see above), mean

368 modularity was almost identical whatever the crop considered, at about 0.5. At an equal

369 sampling survey effort of 85 fields, modularity was 0.43 ($CI_{95\%}$: 0.39–0.47) for meadows,

370 0.45 (0.40–0.49) for SF and 0.48 (0.45–0.52) for OSR. With a higher sampling rate (n = 165

371 fields), but at the cost of losing crop types in the comparisons, OSR showed significant higher

372 modularity values than SF. The two mass-flowering crops' networks also had very different

373 specialisation (H2'), showing the two most extreme values among our six crops. OSR was far

374 less specialised (0.31 (0.29–0.33) at 165 fields) than all other crops, while SF (0.58 (0.55–

375 0.61)) showed the most specialised network; the other crops showed intermediate values, *e.g.*

376 0.45 (0.43–0.47) for meadows and 0.40 (0.34–0.46) for cereals at a survey effort of 85 fields.

377 Low specialisation in OSR could be partially explained by the low specialisation of the most

378 abundant insect, the honeybee (d' = 0.27) and the low specialisation of the crop flower, OSR

379 (d' = 0.21). Indeed, in OSR, the average d' of all species was 0.26 for insects (n = 97, median

380 = 0.20) and 0.23 for plants (n = 68, median = 0.44), meaning that the network was lowly

381 specialised at both trophic levels and highly driven by the honeybee and OSR flower

382 dominance. In SF, specialisation was 0.67 for SF (more than three times higher than in OSR)

383 and 0.42 for the honeybee (1.5-times higher than in OSR). SF was thus highly connected to

384 honeybees despite honeybees being slightly less specialised than SF, indicating a larger

385 partners' spectrum. The average d' of all insect species in SF was 0.41 (n = 109, median =

386 0.50) and 0.67 for plants (n = 65, median = 0.51), again reflecting the preponderant roles of

387 honeybees and SF. Nestedness (NODF) increased with sampling effort, being higher in OSR

388 than in any other crops (mean value of 29.8 (22.5–36.8) when sampling effort was low, i.e. 35

16

389 fields), especially in meadows (16.1 (11.0–21.3)), cereals (21.3 (15.1–28.4)) and SF (21.6

390 (16.8–29.2)), rather than in alfalfa (25.5 (21.0–30.8)). When increasing sampling effort (85-

391 field threshold), nestedness reached 33.0 (27.7–38.2) in OSR networks, c. 25% more than in

392 cereals (23.9 (19.9–28.5)) and in SF (23.4 (19.5–28.1)). Weighted NODF average values

393 showed similar patterns: SF reached a WNODF mean value of 14.5 (13.1–15.7) when

394 considering a threshold of 165 fields, whereas OSR networks peaked on average at 21.6

395 (20.3–22.5).

396

397 4. Discussion

398 The detection of several hundreds of species in the plant–pollinator network indicates that the

399 LTSER ZAPVS is characterised by a high diversity of species despite its intensive farming

400 system. While the honeybee, SF and OSR are by far the species that establish most

401 interactions, they are not necessarily those with the greatest number of interacting partners.

402 Although OSR flower is the species with the highest degree (number of interaction partners),

403 confirming its structuring role in the network (Diekötter et al., 2010; Stanley and Stout, 2014),

404 it is closely followed by wild plant species, generally hosted in less-intensively managed but

405 more diverse crops such as alfalfa or meadows. Moreover, the hoverfly *Sphaerophoria scripta*

406 showed far more partners than honeybee, including OSR and SF flowers, suggesting that its

407 role in the network has to be explored in more detail. *Bombus* species are also frequent

408 visitors of SF, as Syrphidae of OSR (Jauker and Wolters, 2008). Although these are rarely

409 studied as key species in networks, they might be strongly involved in OSR and SF

410 pollination (Breeze et al., 2011), and could act as pollination insurance if honeybees were to

411 decline dramatically (Sánchez-Bayo and Wyckhuys, 2019).

412 Completeness of survey effort was, however, moderate: 65% for insects but 80% for plants

413 according to the Chao 2 estimator, despite our dataset covering six months (from April to

17

September) and six years. The phenology of some plants and insects being very short may explain why not all species were detected, in addition to the classic and inherently imperfect detection method. In addition, the low connectance within crops (around 2–3%) suggests that few interactions are carried out among all possible ones. These forbidden links (Jordano, 2016) could result from spatial or temporal constraints (Valdovinos, 2019). Indeed, one of our possible explanations is that each crop network corresponds to a set of different fields that belongs to different landscape entities and different sampling weeks, which generates a high community variability in terms of phenology and location. But a low connectance, i.e. high proportion of forbidden links, is in certain cases one of the indicators of destabilised networks (Landi et al., 2018).

The hypothesis of the dominance of honeybee interactions with crop flowers during OSR flowering and SF flowering, and not in other periods, was largely verified. Overdominance of managed species may destabilise networks (Valido et al., 2019). The stability of a network can be evaluated through the values of some network metrics (Thébault and Fontaine, 2010). A stable bipartite mutualistic network is often a network with a high connectance and many species, as well as a nested – but not very modular – network (Thébault and Fontaine, 2010). In our case, connectance was always very low (<5%), whether we considered the total network or the subnetworks per season or per crop. When the connectance is so low, modularity and nestedness are usually positively correlated (Fortuna et al., 2010), hence a situation with a nested but not modular network is unlikely, therefore possibly suggesting instability in our networks. In particular, the corn–sorghum network, which is highly modular and comprises few species, may show particularly low stability, though we had relatively small sample sizes. Meadows were a special case, endowed with a large number of species but not very nested and not very connected compared to other crops. Thus, although meadow networks appear to be resilient networks thanks to the number of species they host (Okuyama

18

439   and Holland, 2008), they display a certain vulnerability because the sharing of partners is

440   weak, like in the studied SF crops, but contrary to the OSR crops.

441   Indeed, the most striking differences in networks were found between OSR and SF, both

442   being mass-flowering crops. As expected, these two crops drove the overall behaviour of

443   networks during their blooming season (approximately the same metrics of behaviour

444   between the OSR crop and OSR period, and between the SF crop and SF period), although the

445   meadows, weeds in cereals, and alfalfa were flowering at the same time. However, the OSR

446   and SF crops' networks were somewhat opposed in some of the key metrics, hence possibly

447   showing different network stability (Duchenne et al., 2022). The OSR network did not

448   harbour many species, but was highly nested compared to the other crop networks, which

449   therefore suggests it was a resilient network. Its nestedness may result from the fact that the

450   OSR network was mostly composed of species with a high degree of generalisation (i.e. the

451   average species specialisation was quite low in OSR crops), leading to a relatively nested

452   structure (Fontaine et al., 2009). Thus, as the OSR network was the most nested network in

453   our study, it was expected that the general core of species it included were generalists rather

454   than specialists, which was indeed the case. The interaction between OSR and honeybees has

455   a structuring effect for the network, corroborating studies that highlight OSR flower and its

456   partners as a hub that positively influences the visitation and pollination of neighbouring wild

457   plants, especially those with similar morphology (Thompson et al., 2021). OSR is also known

458   to host diverse insect communities (Stanley et al., 2013), while honeybees remain one of the

459   most efficient pollinators and, as demonstrated here, the most important partner of OSR.

460   Conversely, SF appears less stable than OSR because it is much less nested for an equivalent

461   diversity of species, and is composed of more specialised species, including the honeybee–SF

462   duo, which both qualify as specialist species, interacting strongly and almost entirely with

463   each other – a pattern that was not necessarily found in other studies (e.g. Valido et al., 2019).

19

464   Such a quasi-exclusive relationship between honeybees and SF as we found here may reflect

465   either competition within pollinators or plant communities in SF crops, or a strong niche

466   differentiation between wild and managed species. Conversely, OSR may host more

467   generalist species that interact with specialist species and therefore enhance the persistence of

468   the network (Liao et al., 2022).

469

5. Conclusion

471   Our results suggest that the honeybee and crop flower pair may differ between OSR and SF,

472   being an almost exclusive relationship in SF that prevents other partners by competition,

473   while allowing other modules in OSR hence increasing nestedness and consequently

474   improving network stability. This divergence may possibly result from phenological

475   difference, or as a consequence of flower shape – a divergence that can be further explored

476   with species trait approaches.

477

Author Contributions

479   Conceptualisation, V.B. and S.G.; Methodology, C.G., V.B. and S.G.; Formal Analysis, C.G.;

480   Writing-Original Draft Preparation, C.G., S.G. and V.B; Writing-Review and Editing, C.G.,

481   S.G. and V.B. All authors have read and agreed to the published version of the manuscript.

482

Declaration of Competing Interest

484   The authors declare that they have no known competing financial interests or personal

485   relationships that could have appeared to influence the work reported in this paper.

486

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at […]

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Figure legends

Fig. 1

Mean values of number of nodes (±95% confidence intervals) for each crop, according to the number of sampled fields (x-axis). Brown points and line: cereal; Light blue points and line: oilseed rape; Dark green points and line: alfalfa; Dark blue points and line: corn and sorghum; Light green points and line: meadow; Red points and line: sunflower.

Fig. 2

Interaction number (frequency of insects interacting with flower) per hectare and per crop throughout the season. Data are presented as mean±se (standard error). Analyses of variances were run on each fortnight (two weeks aggregated) to compare crops (log+1-transformed). If p-value < 0.001 then ***; If $0.001 \leq$ p-value < 0.01 then **; If $0.01 \leq$ p-value < 0.05 then *; If $0.05 \leq$ p-value < 0.1 then '.' Brown points and line: cereal; Light blue points and line: oilseed rape; Dark green points and line: alfalfa; Dark blue points and line: corn and sorghum; Light green points and line: meadow; Red points and line: sunflower.

Fig. 3

(a) Histograms of species number per crop for pollinator and insect groups. Grey bars: species number of the different plant groups. Blue bar: honeybee species number; Turquoise bar: bumblebee species number; Green bar: other social bee species number; Yellow bar: solitary bee species number; Orange bar: butterfly species number; Pink bar: hoverfly species number. (b) Bipartite representations of crop networks involving the main pollinator taxonomic groups and the main plant groups. Blue path: honeybee interaction; Turquoise path: bumblebee interaction; Green path: other social bee interaction; Yellow path: solitary bee interaction; Orange path: butterfly interaction; Pink path: hoverfly interaction.

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Fig. 4

Interaction number (i.e. each time insect in foraging behaviour was observed on a flower) between main types of pollinator groups (y-axis) and plant species (x-axis), with histograms of the number of interactions per species (log+1 transformed data) ranging from highest species degrees to lowest species degrees (light grey to dark grey). Point size: number of interactions category, from zero to infinity. Blue points: honeybees; Turquoise points: bumblebees; Green points: other social bees; Yellow points: solitary bees; Orange points: butterflies; Pink points: hoverflies.

Fig. 5

Mean network metric values (±95% confidence intervals) for (a) periods and (b) crops, based on the number of sampled fields (x-axis) and with a y-axis scale indicating the value of the metric.

Period metrics; Grey squares: all periods; Purple points: oilseed rape flowering period; Orange points: dearth period; Yellow points: sunflower flowering period.

Crop metrics: Grey squares: all crops; Brown points: cereal crop; Light blue points: oilseed rape crop; Dark green points: alfalfa crop; Dark blue points: corn and sorghum crop; Light green points: meadow. Red points: sunflower crop.